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Shoot growth and crown development: effect of crown position in three-dimensional simulations

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Summary Trees have been increasingly considered as modular organisms, with individual shoots forming autonomous units that respond semi-independently to their surrounding environment. However, there is evidence for fairly strict hormonal control of tree crown development. Studies on the hydraulic architecture of trees suggest a closer functional connection between shoots and crown development than is postulated by the theory of branch autonomy. We studied how shoot growth pattern influences growth and crown architecture in young Scots pine trees simulated by the LIGNUM model assuming that (a) the growth of a shoot mainly depends on its light climate and (b) the growth of a shoot is influenced by its position within the crown. We determined shoot position within the crown based on a recently developed vigor index. The vigor index compares the relative axis cross-sectional area from the base of the tree to each shoot and gives a value of 1 to the pathway of the greatest cross-sectional area. All other shoots attain values between 0 and 1 depending on their cross-sectional areas and the cross-sectional areas of the branches leading there from the main axis. The shoot light climate is characterized by annually intercepted photosynthetically active radiation. We compared the results from simulations (a) and (b) against an independent data set. The addition of a within-shoot position index (the vigor index) to our simulation (simulation b) resulted in a more realistic tree form than that obtained with simulation (a) alone. We discuss the functional significance of the results as well as the possibilities of using an index of shoot position in simulations of crown architecture.

Keywords: modeling, modularity, Pinus sylvestris, tree architecture, vigor index.

Introduction

Crown architecture influences both the light capturing characteristics (Horn 1971, Sprugel 1989, Messier et al. 1999) and the use of growth resources by productive and consuming organs (Mäkelä 1986, Ford et al. 1990, Nikinmaa 1992). Givnish (1988) suggested that the "ecological compensation point" of large trees is at a higher intercepted radiation than that of small trees because of the growing imbalance between consuming and producing organs. By modifying their architecture, trees can influence the proportion of growth resources required in these two types of organs (Givnish 1995, Perttunen et al. 1998). Architectural plasticity is thus an important mechanism of acclimation (Ford 1992), particularly when trees grow in low light understories (Messier and Nikinmaa 2000). Because crown shape acclimation is only semi-reversible, however, a tree's ability to respond favorably to subsequent gap formation may be impeded (Messier et al. 1999).

Tree architecture results from shoot level processes: the emergence and extension of new shoots and the thickening and death of old shoots. Plants can be considered as modular organisms where crown shape results from reiteration of basic structural units over time (Hallé et al. 1978). The physiological control of shoot emergence and growth is not completely understood (e.g., Stafsform 1995). For these reasons, tree architecture models have relied on empirical structural relationships rather than on underlying biological mechanisms (Reffye et al. 1989, Prusinkiewicz and Lindenmayer 1990, Kurth 1994). To approach greater functional realism, the local environment of the growing shoots and their position within a tree's topology is considered (Perttunen et al. 1996, Prusinkiewicz et al. 1996, de Reffye et al. 1997, Kurth and Sloboda 1997).

Goulet et al. (2000) recently developed an index of shoot position (hereafter called Vigor Index (VI)) that, in conjunction with available light, appears to explain shoot growth within tree crowns. The initial rationale for using such an index came from transport considerations. It was assumed that the shoot axis with the largest cross-sectional area would best supply the shoots with water and nutrients. Shoots at the end of these axes would thus have the highest sink strength and larg-

est potential for growth. In a tree crown, a single axis at the base of the stem divides into a number of axes as primary branches separate from the main stem, sub-branches separate from primary branches, etc. From the point of view of transport, each branching divides the resource flow from the soil into discrete components. At subsequent division points, only that proportion of total resources that has entered a particular pathway is divided into further components as a result of further stem branching. Therefore, if we evaluate the soil resource supply to the shoots, we should compare the whole transport pathway from the base of the stem to the shoot in question. The largest proportion of the resource supply goes to the shoot at each junction having the largest proportion of flow. The VI compares each junction and assumes that the thicker axis is favored. Thus, the most rapid shoot growth should occur in the end of axes that are thickest at each division point between the base of the tree and the shoot apex. This also gives the highest value for VI. This formulation of the VI supports the idea that hydraulic architecture maximizes water transport along the main axis (Zimmermann 1983), and that balanced length and diameter growth is needed to maintain mechanical stability (King and Loucks 1978, Givnish 1995).

We investigated the influence of shoot growth pattern on growth rate and crown architecture of young Scots pine trees. We also examined the potential of the VI to provide realistic simulations of tree architecture. We simulated crown architecture development with the LIGNUM model (Perttunen et al. 1996) assuming that (a) shoot growth depends only on the light climate and (b) shoot growth is influenced by position within the crown. We discuss the results in the context of three-dimensional tree growth modeling.

Materials and methods

Description of VI

To calculate VI, we follow the woody axis from the base of the tree to the shoot of interest. At each branch point along this pathway we compare the thickness of the dividing axes. If the axis being followed is the thickest at the branch point, it is assigned a value of 1. Otherwise it is assigned a value reflecting the ratio between the cross-sectional areas of the axis of interest and the thickest axis at the branch point. The axis of interest retains this value until the next branch point, and the calculation is repeated. This procedure is continued until the shoot at the tip of the axis is reached (Figure 1).

Denoting the VI value of the axis below the branching point by v_{i-1}, the equation for the VI value at the following branching point i (i = 1, …, n) is:

$$v_i = \left(\frac{d_j}{d_M}\right)^2 v_{i-1}, \quad (1)$$

where d_j is the diameter of axis j and d_M is the diameter of the largest axis of the branching point (d_M = max(d_j|j = 1, ..., n),

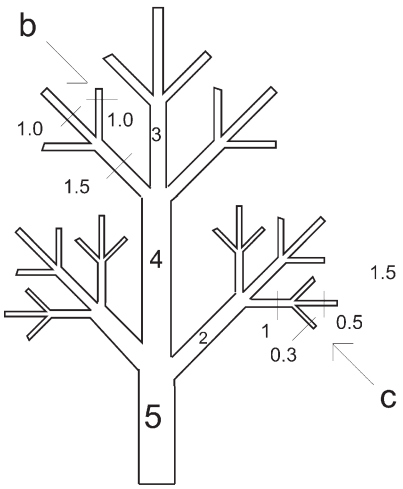

Figure 1. Schematic presentation of the calculation of Vigor Index (VI). The numbers indicate the diameter of tree segments of a hypothetical tree. At each whorl, the main stem is the thickest axis, v_{i+1} = 1(v_i); hence the VI value for the leader shoot is 1 (v_0 at the tree base is 1). Similarly the value of VI for the shoot at point (b) is $(4/4)^2(1.5/3)^2(1/1)^2 = 0.25$ and the VI value for the shoot at point (c) is $(2/4)^2(1/1.5)^2(0.3/0.5)^2 = 0.04$.

where 1, ..., n are the axes at the branching point). Thus the value of VI for a shoot is:

$$\mathrm{VI} = \prod_{i=0}^{n} v_i, \quad (2)$$

where VI is the value of the vigor index for the shoot of interest, i = 0 is the basal section of stem before the first branch point and n is the shoot of interest.

Necessarily, the value of VI decreases as branching order increases. Similarly, branches that are of small diameter relative to the main stem have comparatively low VI values. Furthermore, as the stem tapers, branches in the upper part of the crown have greater VI values than those of similar size in the lower part of the crown.

Relationship between VI and shoot growth

Shoot growth, light climate and the vigor index were measured for 38 shoots of four Scots pine saplings, between 201 and 300 cm tall, growing on the southern edge of a large gap in a *Vaccinium*-type stand in southern Finland (61°51′ N, 24°17′E, 160 m a.s.l.). The shoots were selected to represent different branching orders (from main stem to third-order branches).

The shoot light climate varied between 40 and 60% of the above-canopy condition and was measured during overcast conditions with a hand-held quantum sensor (LI-189, Li-Cor, Lincoln, NE) that was positioned horizontally above the shoot. To provide an estimate of the proportion of irradiation reaching the shoots, the reading was divided by a simultaneous reading measured automatically above the canopy at a distance of 500 m from the seedlings (Parent and Messier 1996).

There was a close linear relationship between shoot extension growth and VI (Figure 2a). Because of the small variation in light climate, no significant effect of light on growth was noted. For each tree, relative shoot growth was calculated in relation to the longest shoot of the seedling. A simple linear regression was fitted between VI values and relative extension growth for use in simulations with the LIGNUM model (Figure 2b). The regression equation for the relative extension growth as a function of VI was $gl_{rel} = 0.044 + 0.925VI$, where gl_{rel} is the relative extension growth of a shoot ($r^2 = 0.91$, F-ratio = 383, $n = 39$; both the intercept and the slope were significant ($P < 0.04$ and $P < 0.001$, respectively)).

Description of LIGNUM model

The LIGNUM model (Perttunen et al. 1996, 1998) generates a tree as a population of shoots connected to a previously formed woody structure that itself results from secondary thickening of previously formed shoots. In the model, shoots are called tree segments. A crown of the model tree consists of tree segments, branching points and buds. Each pair of tree segments is separated by a branching point, as are the buds from the tree segments. A branching point specifies the location of the points of attachments of the different axes of the tree in three-dimensional space. The buds produce new tree segments, branching points and buds (i.e., new shoots). A tree segment may contain sapwood, heartwood, bark and foliage.

Growth of the tree is driven by the quantity of available carbohydrates. Annual photosynthetic production by the crown is linearly proportional to crown light interception. The model calculates annual PAR interception for each shoot for all of the different directions of the sky hemisphere by considering the possible shading of other shoots in those directions. Shading and PAR interception by a shoot is proportional to the PAR incident to it, its foliage density and the distance that light travels through it. Crown-level annual radiation interception is the sum of radiation intercepted by all of the shoots (see Perttunen et al. 1998 for a more detailed explanation).

Carbon consumed for maintenance respiration of all tree organs is subtracted from photosynthetic production to yield carbohydrates available for growth. At the organ level, maintenance respiration rate is calculated by summing the respiration rates of different tissues. Respiration by a given tissue is the product of tissue-specific annual respiration rate and the mass of that tissue type (Perttunen et al. 1996).

Table 1. Parameter values used in the simulations. Some of the values were taken from Perttunen et al. (1998). The values of parameters 1, 4, 8, 10 and 11 were estimated from measurements made in a Scots pine stand close to the trees used for VI determinations.

Name	Unit	Value
1. Leaf mass per shoot cylinder area	kg m^{-2}	1.3
2. Carbon allocation to roots relative to foliage	kg kg^{-1}	0.5
3. Shoot length–diameter relationship		100
4. Maintenance respiration of leaves	kg C kg C^{-1} $year^{-1}$	0.2
5. Maintenance respiration of roots	kg C kg C^{-1} $year^{-1}$	0.24
6. Maintenance respiration of sapwood	kg C kg C^{-1} $year^{-1}$	0.024
7. Annual senescence rate of roots	$year^{-1}$	0.33
8. Annual senescence rate of sapwood	$year^{-1}$	0.07
9. Wood density	kg m^{-3}	400
10. Proportion of primary wood from shoot cross section		0.6
11. Light-use efficiency	kg DM MJ^{-1}	0.001

LIGNUM distinguishes between resource use for shoot extension growth and secondary axis thickening (Perttunen et al. 1996, 1998). Shoot growth triggers secondary wood thickening in the existing axis, but thickening in turn imposes limitations on extension growth by depleting the total resources available for growth. Secondary thickness growth is based on the pipe model; thus, tree ring area growth at any height is proportional to net foliage growth above that height. Shoot foliage mass is proportional to the surface area of the shoot axis and is therefore proportional to the square of the extension growth. Root growth is calculated based on the functional balance principle (Davidson 1969).

Resource use for extension growth depends on the number of new shoots and their extension growth. The number of developing buds depends on mother shoot size. Absolute extension growth depends on the difference between availability of

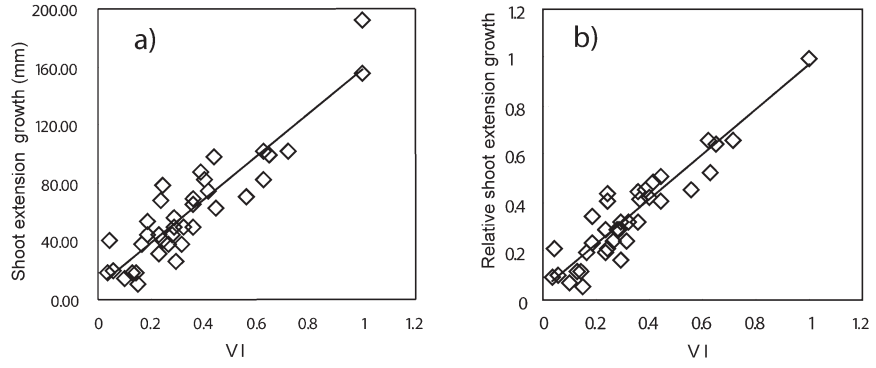

Figure 2. (a) Annual shoot extension of Scots pine as a function of Vigor Index (VI). The regression line is: shoot length = 8.754 + 149.228VI ($r^2 = 0.855$, F-ratio = 225.15, $n = 39$). The relative solar irradiance received by shoots varied between 40 and 60% of open-light conditions but did not significantly affect shoot growth. Data are from four trees at the southern edge of a large gap. (b) Relative shoot extension in relation to the longest measured shoot per tree as a function of VI. The regression line is: $gl_{rel} = 0.044 + 0.925VI$ ($r^2 = 0.91$, F-ratio = 383, $n = 39$; both the intercept and the slope were significant ($P < 0.04$ and $P < 0.001$, respectively)).

photosynthetic products and their use in secondary thickening. Apical buds form 20% larger shoots than lateral buds. Otherwise, shoot growth in different parts of the crown was determined either by shoot light climate only or by light climate and VI. The exact formulation is given in the Appendix.

Simulations

We compared early growth of open-grown Scots pine seedlings with the LIGNUM model using different principles for determining relative shoot extension growth. The simulation parameters were the same as those used by Perttunen et al. (1998), and were determined from empirical measurements taken from a young Scots pine stand that grows in the vicinity of the trees used for VI determination, and from the literature (Table 1). To calculate radiation from different sectors of the sky, we used the zonal brightness function of the standard overcast sky from Ross (1981). Radiation coming from the sectors was scaled so that the insolation (in terms of PAR) equaled 1200 MJ m^{-2} on a horizontal surface. This value is typical for the growing season in southern Finland (Stenberg 1996). In the simulations, each sector had an azimuthal width of 15° and an inclination width of 10°, giving a total of 216 sectors.

The objective of the simulation study was to determine if consideration of the effect of shoot position on shoot extension growth improved description of crown development and form. We simulated tree architecture development assuming that (a) relative shoot growth is influenced only by its light climate without any position effect and (b) light influences shoot growth and there is a position effect as determined by VI.

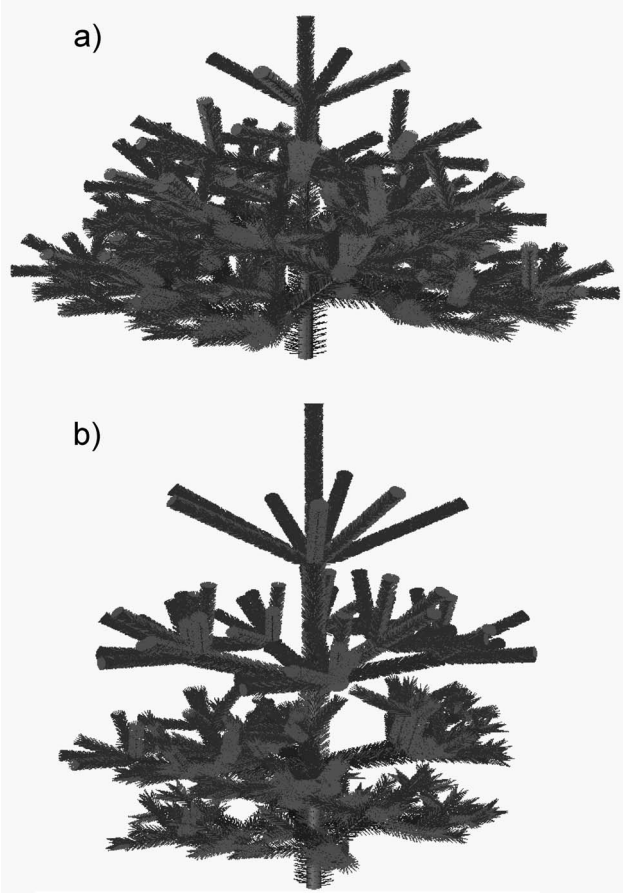

Figure 3. Simulated 5-year-old Scots pine seedling when (a) only light climate influences the relative shoot extension, or (b) light climate and Vigor Index influence the relative shoot extension (the scale of the images has been adjusted to fit them into the same figure).

Results

Figures 3a and 3b illustrate how crown architecture develops assuming that shoot light climate and position influence shoot growth. If no position influence on shoot growth is assumed, the tree crown becomes "bushy" (Figure 3a); height growth from year to year remains fairly constant and extension growth of the lower branches is almost equal to the growth in tree height. When a shoot position constraint was imposed (i.e., VI), the height growth increased whereas the length growth of lower branches decreased over time.

We evaluated the different simulation approaches by comparing the simulated tree crown attributes with measured values. The measured data set consisted of 20 open-grown Scots pine trees from southern Finland collected by Lukkarinen (1992). The trees ranged between 5 and 30 years of age and from 2.34 to 11.4 m in height. The trees were often located at forest edges or agricultural field boundaries, forming a rather heterogeneous group with respect to site conditions. Measurements from each tree included total tree height and longest branch length. Stem disks were cut at 10 proportionately spaced heights from the base to the tip of the tree. Near the base, the heights were 0, 2, 6 and 10% of the total height. The diameter at each height was determined as the mean of two perpendicular measurements.

We compared the simulated relationships between tree height, longest branch length and basal diameter with the observed values. For the observed basal diameter, the value interpolated at 20 cm height was used. The comparison shows that the architecture of simulated trees, for which both light and VI influences were considered, resembled observed trees more closely than simulations in which only light influence was considered. In the former case, simulated tree height and longest branch length were comparable with measured values (Figure 4a). When only light influence was considered, branches were too long when compared with tree height (Figure 4a). As indicated in Figure 4b, the diameter in both simulations increased at a similar rate, indicating that simulated foliage mass was similar. The major difference between the simulations was in height growth. When only the influence of light on shoot growth was considered, the model predicted little height growth of the main stem and growth was divided evenly among the shoots. In contrast, when both light and VI influences on shoot growth were considered, a higher proportion of growth was predicted in the main stem. Based on the comparison between the simulated and observed basal diameters (Figure 4b), height growth was too high when both light

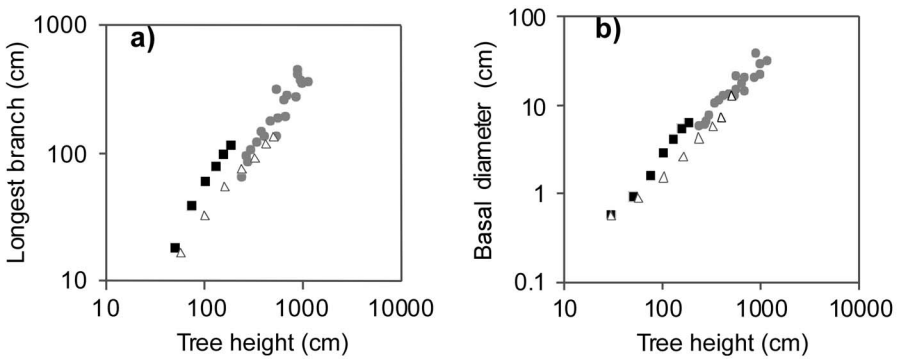

Figure 4. (a) Height versus maximum branch length and (b) height versus basal diameter of open grown seedlings. Boxes denote the development of simulations when only light influences shoot growth and triangles denote the development of simulations when both light and measured Vigor Index influence shoot growth. The solid circles represent field observations by Lukkarinen (1992), with each symbol representing the value of a single tree.

and VI influences were simulated and too low when only light influence was considered. However, the normal basal swelling of trees, which was not considered in the simulations, could help explain some of the differences between the simulated and measured trees. If basal swelling was added to the simulated trees, the VI simulations would more closely approximate the observed values, whereas the light climate simulations would deviate further from the observed values.

Overall, the comparison between the simulated and observed results was promising considering that the model was independently parameterized with measurements done mostly in one location (see Perttunen et al. 1998), whereas the observations were collected from highly heterogeneous conditions and from different areas in southern Finland (Lukkarinen 1992).

Figure 5 illustrates how the choice of different values for VI affects crown shape (see Appendix for details). Figure 5a is the same as Figure 3b, Figure 5b describes crown shape development for a reduced VI influence and Figure 5c describes crown shape development for increased VI influence. As the VI influence is reduced, crown shape increasingly resembles that produced when shoot growth is influenced only by light.

Discussion

Trees have been increasingly viewed as modular organisms and their reiterative pattern of simple structures repeating over time identified as the process responsible for tree crown development (e.g., Hallé et al. 1978). Many physiological studies have revealed that branches are autonomous with respect to their carbon requirement (e.g., Dickson and Isebrands 1991), suggesting that individual shoot development could be viewed as a locally occurring process, with photosynthetic production efficiency playing a key role (Linder and Axelsson 1982).

Another view of trees is based on the connectivity of different tree organs. The concept of an integrated physiological unit (IPU, Watson and Casper 1984) stresses the importance of a balanced supply and transport of both above- and belowground resources for undisturbed tree functioning. According to this view, tree growth is the development of integrated leaf–wood–root units. Modeling of tree carbon allocation based on pipe model principles (Valentine 1985, Mäkelä 1986) represents a closely related concept.

Common to the IPU or pipe model approach and that of mechanical support (e.g., Kellomäki and Strandman 1995) is the

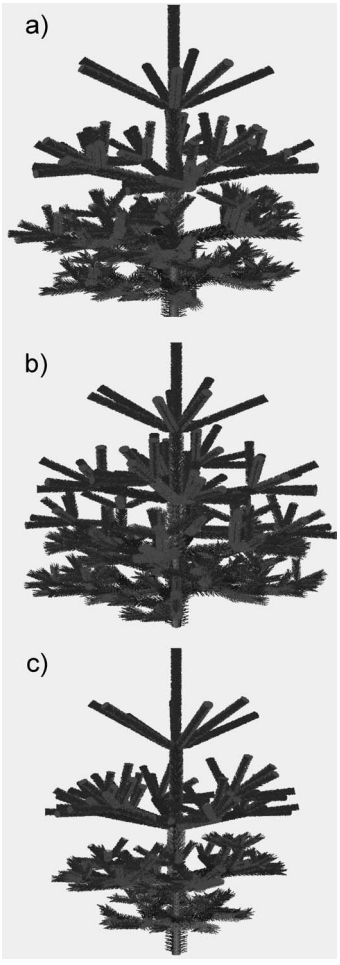

Figure 5. Simulated 5-year-old Scots pine seedlings when (a) light and Vigor Index (VI) influence the relative shoot growth (as in Figure 3b), (b) the VI influence is smaller than in (a), and (c) the VI influence is stronger than in (a). The scale of the tree images has been varied to fit them into the same figure.

idea that growth of leaves is associated with secondary wood thickening and root growth. Foliage at different heights (i.e., different distances from the roots) has different carbon consumption requirements (Stevens and Perkins 1992). Investment in leaves at low heights allows a larger proportion of photosynthetic production to be used for foliage growth compared with investment higher up in the canopy, because wood growth is proportional to both net foliage growth and the distance between foliage and roots. However, in a competitive environment, foliage is also likely to be shaded, possibly resulting in lower net foliage growth. Depending on the competitive environment, different height growth strategies are favored (Givnish 1995). Game theory has been applied to study height growth strategies (Mäkelä 1985, Givnish 1986), but an optimal allocation for different conditions can also be formulated (Nikinmaa 1992).

Thus shoots grown in the upper and lower parts of the tree crown play different roles in crown dynamics. Because young, first-order shoots in the upper crown are unlikely to be immediately shaded, they play an important role in supporting tree structure for many years. On the other hand, shoots in the lower crown, even if at first in a strong light environment, become shaded and less able to support other shoots. Therefore, we postulated that there are mechanisms facilitating the control of shoot growth in relation to shoot position for trees that normally compete for light during canopy development.

The VI described the apical control of tree crown development fairly well, even though the underlying functional mechanisms are unclear. That larger branches grow more vigorously is evident, but the VI also predicts that a lower branch grows less than an upper branch given similar size and light conditions. Assuming that similar sized branches also have similar foliage areas, this would mean that, under similar irradiation conditions, lower branches allocate less of their production to their own growth than do upper branches.

According to our simulations, with increasing VI influence, crowns become narrower and side branches shorter. Part of the rationale for using the VI came from consideration of the hydraulic architecture of trees (Goulet et al. 2000). Based on Zimmermann's ideas (1983), the (thicker) main axis is hydraulically preferred and this is reflected in increased transpiration rates, increased supply of nutrients with the transpiration stream, increased carbon uptake rate and increased growth. In dry soils, the water potential of shoots needs to increase to maintain the same transpiration (and photosynthetic) rate (Sperry 1995). In those parts of the crown that have low leaf specific water conductivity (e.g., side branches, Zimmermann 1983), the shoot water potential would increase the most, which may result in stomatal closure to avoid cavitation (Williams et al. 1996). The closing of stomata in one part of the crown would facilitate transpiration in the other crown parts (Whitehead et al. 1996). Therefore, if there are permeability changes between the main (thicker) axis and the side axes, trees that are growing on dry soils will have larger differences between main axis and side axis growth than trees growing on moist sites with good water availability. In terms of VI, the influence on shoot growth should be stronger on dry sites than on wet sites. In the context of our simulation results, the Scots pine crown should be narrower on dry sites than on wet sites because of the effect of VI.

More work needs to be done to test the general applicability of our proposed VI. As Goulet et al. (2000) noted, different developmental patterns in xylem structure may affect the relationship between shoot axis growth and its vigor index. However, VI is a potentially useful tool for making crown development estimations. If VI is generally applicable, it could be used with models to simulate the three-dimensional development of tree crowns. The ease of measuring VI facilitates determination of its influence for various species, thus providing a means of simulating the influence of crown dynamics in mixed species stands.

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References

Davidson, R.L. 1969. Effect of root/leaf temperature on root/shoot ratios in some pasture grasses and clover. Ann. Bot. 33:561–569.

de Reffye, P., C. Edelin and M. Jaeger. 1989. La modélisation de la croissance des plantes. Recherche 20:158–168.

de Reffye, P., T. Fourcaud, F. Blaise, D. Barthélémy and F. Houllier. 1997. A functional model of tree growth and tree architecture. Silva Fenn. 31:297–311.

Dickson, R.E. and J.G. Isebrands. 1991. Leaves as regulators of stress responses. *In* Response of Plants to Multiple Stresses. Eds. H.A. Mooney, W.E. Winner and E.J. Pell. Academic Press, San Diego, pp 4–34.

Ford, E.D. 1992. The control of tree structure and productivity through the interaction of morphological development and physiological processes. Int. J. Plant. Sci. 153:S147–S162.

Ford, E.D., A. Avery and R. Ford. 1990. Simulation of branch growth in the *Pinaceae*: interactions of morphology, phenology, foliage productivity and the requirement for structural support, on the export of carbon. J. Theor. Biol. 146:15–36.

Givnish, T.J. 1986. Biomechanical constraints on crown geometry in forest herbs. *In* On the Economy of Plant Form and Function. Ed. T.J. Givnish. Cambridge University Press, Cambridge, pp 525–583.

Givnish, T.J. 1988. Adaptations to sun vs. shade: a whole plant perspective. Aust. J. Plant Physiol. 15:63–92.

Givnish, T.J. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. *In* Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, San Diego, pp 3–49.

Goulet, J., C. Messier and E. Nikinmaa. 2000. Effect of branch position and light availability on branch segment growth of understory sugar maple and yellow birch saplings. Can. J. Bot. 78:1077–1085.

Hallé, F., R.A.A. Oldeman and P.B. Tomlinson. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, Berlin, 441 p.

Horn, H.S. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, 144 p.

Kellomäki, S. and H. Strandman. 1995. A model for the structural growth of young Scots pine crowns based on light interception by shoots. Ecol. Model. 80:237–250.

King, D. and O.L. Loucks. 1978. The theory of tree bole and branch form. Radiat. Environ. Biophys. 5:141–165.

Kurth, W. 1994. Growth Grammar Interpreter GROGRA 2.4. A software tool for the 3-dimensional interpretation of stochastic, sensitive growth grammars in the context of plant modelling. Introduction and reference manual. Berichte des Fortschungszentrums Waldökosysteme, Ser. B38, Göttingen, 192 p.

Kurth, W. and B. Sloboda. 1997. Growth grammars simulating trees —an extension of L-systems incorporating local variables and sensitivity. Silva Fenn. 31:285–295.

Linder, S. and B. Axelsson. 1982. Changes in carbon uptake and allocation patterns as a result of irrigation and fertilization in young *Pinus sylvestris* stands. *In* Carbon Uptake and Allocation in Sub-alpine Ecosystems as a Key to Management. Ed. R.H. Waring. Forestry Research Laboratory, Corvallis, OR, pp 38–44.

Lukkarinen, E. 1992. Männyn pituus ja paksuuskasvun suhde (The relationship between height and diameter growth of Scots pine). M.Sc. Thesis, Univ. Helsinki, Dept. of Forestry Research Management, 47 p.

Mäkelä, A. 1985. Differential games in evolutionary ecology: height growth strategies of trees. Theor. Popul. Biol. 27:239–267.

Mäkelä, A. 1986. Implications of the pipe model theory on dry matter partitioning and height growth of trees. J. Theor. Biol. 123: 103–120.

Messier, C. and E. Nikinmaa. 2000. Effects of light availability and sapling size on the growth, biomass allocation and crown morphology of understory sugar maple, yellow birch and beech. Ecoscience 7:345–356.

Messier, C., R. Doucet, J.-C. Ruel, Y. Claveau, C. Kelly and M. Lechowicz. 1999. Functional ecology of advanced regeneration in relation to light in boreal forests. Can. J. For. Res. 29:812–823.

Nikinmaa, E. 1992. Analyses of the growth of Scots pine: matching structure with function. Acta For. Fenn. 235:1–64.

Parent, S. and C. Messier. 1996. A simple and efficient method to estimate microsite light availability under forest canopy. Can. J. For. Res. 26:151–154.

Perttunen, J., R. Sievänen, E. Nikinmaa, H. Salminen, H. Saarenmaa and J. Väkevä. 1996. LIGNUM: A tree model based on simple structural units. Ann. Bot. 77:87–98.

Perttunen, J., R. Sievänen and E. Nikinmaa. 1998. LIGNUM: A model combining the structure and functioning of trees. Ecol. Model. 108:189–198.

Prusinkiewicz, P. and A. Lindenmayer. 1990. The algorithmic beauty of plants. Springer-Verlag, Berlin, 228 p.

Prusinkiewicz, P., M. Hammel, J. Hanan and R. Mech. 1996. Visual models of plant development. *In* Handbook of Formal Languages. Vol. 3. Eds. G. Rozenberg and A. Salomaa. Springer, Berlin, pp 535–597.

Ross, J. 1981. The radiation regime and architecture of plant stands. W. Junk Publishers, The Hague, 391 p.

Sperry, J.S. 1995. Limitations on stem water transport and their consequences. *In* Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, San Diego, pp 105–124.

Sprugel, D. 1989. The relationship of evergreenness, crown architecture, and leaf size. Am. Nat. 133:465–479.

Stafsform, J.P. 1995. Developmental potential of shoot buds. *In* Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, San Diego, pp 257–279.

Stenberg, P. 1996. Metsikön rakenne, säteilyolot ja tuotos (Stand structure, radiation and production). Univ. Helsinki, Dept. of Forestry Ecology Publications 15, 68 p.

Stevens, G.C. and A.L. Perkins. 1992. The branching habits and life history of woody plants. Am. Nat. 139:267–275.

Valentine, H.T. 1985. Tree-growth models: derivations employing the pipe model theory. J. Theor. Biol. 117:579–584.

Watson, M. and B.B. Casper. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. Ann. Rev. Ecol. Syst. 15: 233–258.

Whitehead, D., N.J. Livingston, F.M. Kelliher, K.P. Hogan, S. Pepin, T.M. McSeveny and J.N. Byers. 1996. Response of transpiration and photosynthesis to a transient change in illuminated foliage area for a *Pinus radiata* D. Don tree. Plant Cell Environ. 19:949–957.

Williams, M., E.B. Rastetter, D.N. Fernandes et al. 1996. Modeling the soil–plant–atmosphere continuum in a *Quercus–Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. Plant Cell Environ. 19:911–927.

Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, 143 p.

Appendix

The LIGNUM model calculates the relative shoot growth (L_{rel}) as a function of shoot light climate ($f_l(I_p)$) and its position within the tree's topology (f_p) (see Perttunen et al. 1996, 1998):

$$L_{rel} = (f_l(I_p))\, f_p. \quad \text{(A1)}$$

In the simulations, we used the light climate functions as described by Perttunen et al. (1998):

$$f_l(I_p) = 0 \text{ if } I_p < 0.4 \quad \text{(A2)}$$

$$f_l(I_p) = 1.67 I_p - 0.67 \text{ if } I_p > 0.4,$$

where

$$I_p = I_v / I_0, \quad \text{(A3)}$$

I_v is the radiation (from all directions) intercepted by the shoot, and I_0 is the radiation intercepted by an identical but unshaded shoot.

For the position influence in the simulations (Figures 3b and 5a–5c) we used the apical dominance and the VI to describe the effect of topology. For the terminal bud:

$$f_p = f(\mathrm{VI}). \quad \text{(A4)}$$

For all other buds forking from the same branching point,

$$f_p = (1-a)\, f(\mathrm{VI}), \quad \text{(A5)}$$

where a is a parameter that represents the apical dominance effect. In the simulations, a value of 0.2 was used. The following expressions were used for the vigor index (VI):

$$f(\mathrm{VI}) = 0.05 + 0.95\,\mathrm{VI} \quad \text{(A6)}$$

for Figures 3c and 5a,

$$f(\mathrm{VI}) = 0.15 + 0.85\,\mathrm{VI} \qquad \text{(A7)}$$

for Figure 5b, and

$$f(\mathrm{VI}) = \max(0, -0.05 + 1.05\,\mathrm{VI}) \qquad \text{(A8)}$$

for Figure 5c.